

# Species abundance: from neutral to niche-stabilized communities

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## Abstract

We study a stochastic community model able to interpolate from a neutral regime to a niche partitioned regime upon varying a single parameter, tuning the relative strength of intraspecific and interspecific competition. By means of a self-consistent approach, we obtain an analytical expression for the species abundance distribution, in excellent agreement with stochastic simulations of the model. In the neutral limit, such calculation recovers the Fisher log-series. In the niche-dominated regime, the species abundance distribution develops a maximum at a finite population size, corresponding to the emergence of a carrying capacity. We also investigate numerically species extinction-time distribution and compare it with the neutral case. We find that enhanced competition increases the species lifetimes on average while suppressing their fluctuations. The results are discussed in view of the niche-neutral debate and of their potential relevance to field data.

**Key words:** Neutral Theory, Niche Theory, Competition, Species Abundance Distribution, Species Lifetimes

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## 1. Introduction

Understanding the forces shaping ecological communities and promoting species coexistence is a key longstanding issue in theoretical ecology. Niche theory (MacArthur and Levins, 1967a; Chesson, 2000; Chase and Leibold, 2003) and neutral theory (Caswell, 1976; Bell, 2001; Hubbell, 2001) propose two alternative mechanisms for explaining long-term coexistence of species communities.

Many observational studies have highlighted the importance of specificities in resource exploitation and thus of niche differentiation for long-term coexistence (see Wright, 2002; Silvertown, 2004, for two recent reviews). From a theoretical point of view, niche partitioning enhances competition with conspecific. As a consequence, species limit their own populations more than those of other species thus promoting coexistence (Chesson, 2000). A simple mathematical formalization of this idea is provided by the Lotka-Volterra competition model (MacArthur and Levins, 1967a), where coexistence emerges whenever intraspecific interactions overtake interspecific ones.

Apparently on the other side of the Moon, ecological neutral theory (Hubbell, 2001) completely disregards species differences and assumes functional equivalence at the individual level. Within this theoretical approach, stochasticity is the leading ecological force, and species coexistence is the result of a dynamical balance between immi-

gration/speciation processes and extinction. Thanks to the drastic assumptions of neutral theory, ecological patterns such as species abundance relations can be analytically computed in this framework. These predictions, depending on few parameters, fit surprisingly well observational data from tropical forests (see, e.g., Hubbell, 2001; Volkov et al., 2003, 2005).

Due to its strong departure from traditional theoretical approaches, the neutral theory elicited a heated debate in community ecology about its validity and interpretation. A complication is that, in many cases, niche-based and neutral models yield compatible fits of biodiversity patterns (see, e.g., Chave et al., 2002; McGill, 2003; Mouquet and Loreau, 2003; Tilman, 2004; McGill et al., 2006).

Here, we do not enter this debate, but embrace the view that “niche and neutral models are in reality two ends of a continuum with the truth most likely in the middle” (Chase and Leibold, 2003). Indeed, the ecological forces underlying niche and neutral models are not by no means mutually exclusive. Following a similar view, different authors have been proposing models synthesizing niche-based and neutral mechanisms (Tilman, 2004; Leibold and McPeek, 2006; Gravel et al., 2006; Adler et al., 2007; Kadmon, 2007; Pigolotti and Cencini, 2010; Haegeman and Loreau, 2011; Noble et al., 2011a,b). A desired property of these models is the possibility to recover pure neutrality as a limiting case (Alonso et al., 2006), allowing for studying the transi-

tion from niche-dominated to neutral regime when one (or more) ecological parameter is varied. A related issue concerns the robustness of the neutral theory. In particular, a general understanding of whether small non-neutral effects can undermine neutral predictions is still lacking. Finally, niche-neutral models could help our understanding of the dynamical features and long time behavior of ecosystems. Indeed, while neutral theory in principle allows for extrapolating ecosystem behavior at large time-scales (Pigolotti et al, 2005; Azaele et al, 2006; Bertuzzo et al., 2011), an open issue is that predicted species lifetimes tend to be too short compared to fossil records estimates (see, e.g. Lande et al, 2003; Ricklefs, 2003; Nee, 2005; Ricklefs, 2006; Allen and Savage, 2007)

A difficulty with the above program is that usually such mixed models are very hard to analyze mathematically (see, e.g., Tilman, 2004). In this respect, surely, one of the reasons of success of the neutral theory has been its mathematical tractability, i.e. the fact that closed expression for distribution such as species abundance distributions (SAD) can be obtained and easily compared with data (Volkov et al., 2003, 2005). This is usually not possible in models where the neutral hypothesis is broken. Moreover, breaking the neutral hypothesis often leads to a proliferation of parameters, making general comparisons problematic.

As discussed by Adler et al. (2007), neutrality can be violated both at the level of fitness inequalities among the species and/or by the presence of stabilizing processes causing species to limit themselves more than they limit others. These are the two main mechanisms for coexistence identified by Chesson (2000). As for the former kind of violation, Zhang and Lin (1997); Zhou and Zhang (2008) have shown that even small differences in fitness in an otherwise neutral model cause strong reduction of biodiversity. This result is not unexpected as fitness differences, in the absence of stabilizing effects, clearly lead to competitive exclusion. As for the second kind of violation of neutrality, quite interesting is the approach followed by Haegeman and Loreau (2011) who added demographic stochasticity and immigration to classical competitive Lotka-Volterra dynamics with symmetric interactions. A slightly more general model, developed in (Noble et al., 2011a,b; Noble and Fagan, 2011c), incorporates both fitness inequalities and stabilizing mechanisms. In a nutshell, Noble et al. added a frequency-dependent birth rate to the Moran model in a such a way that it reduces to Hubbell's neutral model in an appropriate limit and recovers standard Lotka-Volterra phenomenology in the deterministic limit. They mostly explored ecosystems with few species, aiming at understanding niche stabilization effects at intermediate time scales.

In this paper we investigate a simple variant of the model introduced by Noble et al. (2011b) (see also Noble and Fagan, 2011c). In particular, we focus on communities subject to speciation, death and reproduction where fitness inequalities are disregarded, while stabilizing mechanisms are retained via symmetric interactions as in Haegeman and Loreau (2011). Indeed field data studies (see. e.g.,

Volkov et al., 2009, for a recent study in this direction) support the idea that the most relevant deviation from neutrality consists in differences between intraspecific and interspecific competition. Such differences are usually explained in terms of species-specific resource consumption or more sophisticated mechanisms like Janzen-Connell effects (Janzen, 1970; Connell, 1971).

By means of a self-consistent computation, we derive a closed expression for SAD, depending on a single parameter which quantifies the deviation from neutrality. In the neutral limit, the classical Fisher log-series Hubbell (2001) is recovered. Out of the neutral limit, competitive interactions are essentially incorporated into a single self-consistently derived quantity, which modifies the Hubbell's fundamental biodiversity parameter. Predicted SAD are successfully compared with numerical simulations. Moreover, we study the species extinction time statistics as a function of the strength of the stabilizing effects.

Model details are summarized in Sec. 2. Section 3 presents the main results: the analytical derivation of the SAD with numerical validation, and a numerical study of the species extinction times distribution as a function of the deviation from neutrality. Section 4 is devoted to discussing the results. The Appendix contains some technical details of the self-consistent derivation presented in Sec. 3.

## 2. Model

For the sake of simplicity, we start by introducing the neutral version of the model, which is the standard Moran model for a community with a fixed number,  $J$ , of individuals. At each timestep an individual, randomly chosen among the  $J$  composing the community, is killed. With probability  $\nu$ , it is replaced with an individual belonging to a new species, not present in the system (speciation). With probability  $(1 - \nu)$ , it is replaced with a copy of one of the  $J - 1$  individuals already present in the community (reproduction). Denoting with  $n_i$  the number of individuals of species  $i = 1, \dots, S$  ( $S$  being the number of species currently in the system) present at time  $t$ , the death of an individual of species  $j$  followed by the birth of one of species  $i$  happens at rate

$$(1 - \nu) \frac{n_j}{J} \frac{n_i}{J - 1}, \quad (1)$$

with  $n_i, n_j \geq 1$ .

We now move to the general non-neutral case. Following Noble et al. (2011b), non-neutrality is introduced by biasing reproduction. We introduce the frequency-dependent weights

$$w_i = r_i e^{-\sum_{j=1}^S a_{ij} n_j}, \quad (2)$$

and substitute the term  $n_i/(J - 1)$  of Eq. (1) with

$$\frac{w_i n_i}{\sum_{k=1}^S w_k n_k}, \quad (3)$$

where  $r_i$  models the intrinsic fitness advantage of species  $i$  and  $a_{ij}$  the competition among the species present in the

community. With equal fitness  $r_i = r$  and uniform competition  $a_{ij} = a_j$ , Eq. (3) reduces to the neutral value  $n_i/(J-1)$  (by definition  $\sum_{k=1}^S n_k = J-1$  as the dead individual does not participate to reproduction). In a different limit, one can draw a correspondence with the Lotka-Volterra competitive model by expanding (3) for small  $a_{ij}$  and neglecting fluctuations (Noble et al., 2011b; Noble and Fagan, 2011c).

Specifically, we consider a simplified variant of the model by imposing equal fitness  $r_i = r$  while retaining niche-stabilization (Adler et al., 2007) through a fully symmetric competition matrix  $a_{ij} = a\delta_{ij} + b(1-\delta_{ij})$ , as in Haegeman and Loreau (2011). With these simplifications, Eq. (3) reduces to

$$\frac{n_i e^{-an_i - b \sum_{j \neq i} n_j}}{\sum_{k=1}^S n_k e^{-an_k - b \sum_{j \neq k} n_j}} = \frac{n_i e^{-(a-b)n_i}}{\sum_{k=1}^S n_k e^{-(a-b)n_k}}, \quad (4)$$

where we used  $\sum_{j \neq i} n_j = (J-1) - n_i$ . Parameters  $a$  and  $b$  tune the weights of intraspecific and interspecific competition, respectively. Finally, by defining  $c = a - b$ , the frequency-dependent rates can be written as

$$\omega^{(i)}(n_i) = \frac{n_i e^{-cn_i}}{\sum_{k=1}^S n_k e^{-cn_k}}, \quad (5)$$

where  $c$  fully specifies the deviation from the neutral case, corresponding to  $c = 0$ .

We focus on the case  $c > 0$ , meaning intraspecific competition being stronger than interspecific one (i.e.  $a > b$ ), as observed in real data (Volkov et al., 2009).

### 3. Results

In this section we present the main results. First, we show that the species abundance distribution (SAD) of the model can be analytically computed by means of an approach similar to that used in Volkov et al. (2003) for the neutral model, complemented with a self-consistent ansatz for the treatment of non-neutral competitive interactions. Second, we study the dynamical properties of the model by numerically investigating the single species extinction times statistics.

#### 3.1. Species abundance distribution

Within the model introduced in Sect. 2, the dynamics of the population of a species, labeled  $i$ , is ruled by the master equation

$$\frac{d}{dt} p_n^{(i)}(t) = b_{n-1}^{(i)} p_{n-1}^{(i)} + d_{n+1}^{(i)} p_{n+1}^{(i)} - (b_n^{(i)} + d_n^{(i)}) p_n^{(i)}, \quad (6)$$

where  $p_n^{(i)}(t)$  is the probability for species  $i$  of having  $n_i = n$  individuals at time  $t$ . The death and birth probabilities  $d_n^{(i)}$  and  $b_n^{(i)}$  depend on the species populations and can be expressed as follows. The former is completely neutral and determined by the relative population of species  $i$

$$d_n^{(i)} = \frac{n_i}{J}. \quad (7)$$

The latter, instead, explicitly accounts for competition with the other species and reads

$$b_n^{(i)} = (1-\nu)\omega^{(i)}(n_i) = (1-\nu) \frac{n_i e^{-cn_i}}{\sum_{k=1}^S n_k e^{-cn_k}}. \quad (8)$$

The complication with respect to the neutral case is that, now, the master equation for the focal species depends on the populations of all the others. Notice that, in Eq. (8), the birth probability  $\omega^{(i)}(n)$  is decreased by the factor  $(1-\nu)$  to account for speciation, which from the point of view of the focal species corresponds to the possibility to give birth to an individual of a new species. Following Volkov et al. (2003) we set  $b_0^{(i)} = \nu$  (accounting for the appearing of the species) and  $b_{-1}^{(i)} = 0$ . It is worth underlining that, with this representation, the total number of individuals is not fixed, which is a good approximation when both the total population size  $J$  and the number of species  $S$  are large.

Imposing the detailed balance, the equilibrium distribution can be written as

$$p_k^{(i)} = \theta \prod_{j=1}^k \frac{b_{j-1}^{(i)}}{d_j^{(i)}} = \theta \frac{J^k (1-\nu)^k e^{-\frac{c}{2}k(k-1)}}{k \prod_{j=1}^k \sum_{l=1; l \neq j}^S n_l e^{-cn_l}}. \quad (9)$$

However, unlike the neutral case, expression (9) does not solve the problem as it represents just a formal solution, valid for given values of the populations of the other species  $n_l$  (with  $l \neq i$ ), which are unknown. The normalization factor  $\theta$  is introduced in analogy with the “fundamental biodiversity number” in Hubbell’s model (Hubbell, 2001) and will be made explicit below.

To solve the problem, we can now exploit the species-level symmetry of the model and make the ansatz that all species have the same equilibrium distribution, thus dropping the dependence on  $i$ , i.e.  $p_k^{(i)} = p_k$ . Further, if parameters are such that  $S$  is sufficiently large, we can assume that the  $n_l$  are uncorrelated random variables. These two assumptions are sufficient to find the solution to our problem self-consistently. Upon defining the generating function of the equilibrium distribution

$$\tilde{p}(z) = \sum_{k=1}^{\infty} p_k e^{-zk} \quad (10)$$

and under the two assumptions above, we can simplify the denominator of (9), yielding

$$p_k = \theta \frac{J^k (1-\nu)^k e^{-\frac{c}{2}k(k-1)}}{k [-S\tilde{p}'(c)]^k}, \quad (11)$$

where the prime denotes derivative, so that  $\tilde{p}'(c) = \sum_{k=1}^{\infty} p_k k e^{-ck}$ . Notice that  $-S\tilde{p}'(0) = S\langle n \rangle = J$ , so that we can rewrite the equilibrium distribution more compactly as

$$p_k = \theta \frac{[(1-\nu)g]^k}{k} e^{-\frac{c}{2}k(k-1)}, \quad (12)$$

where  $g = \tilde{p}'(0)/\tilde{p}'(c)$ . Equation (12) provides an analytical expression for the  $\{p_k\}'s$  as a function of the deviation

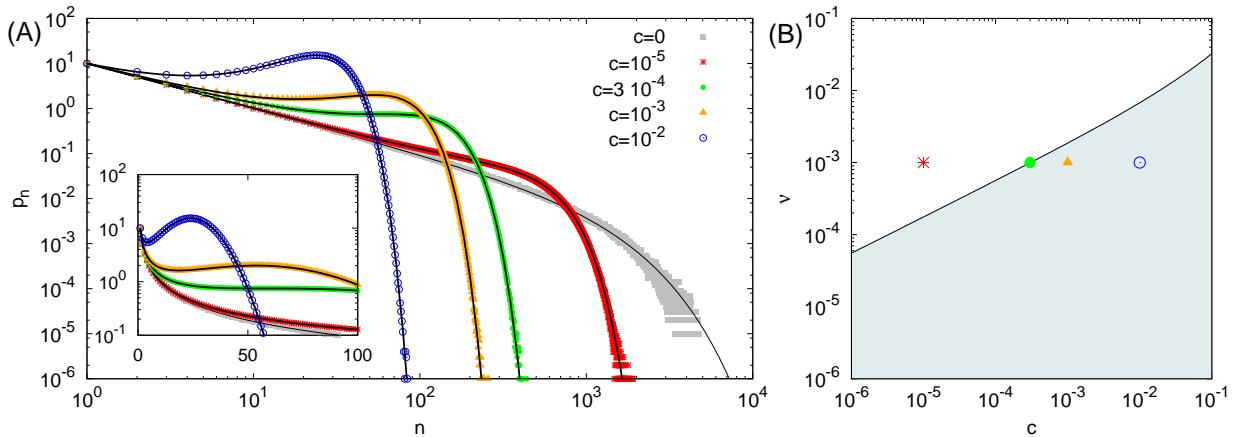


Fig. 1. (A) Species abundance distribution at varying the competition intensity  $c$  as in the legend. Inset: zoom of the same curves in log-lin scale to highlight the emergence of a mode. Symbols refer to simulations and solid curves to the prediction (12). (B) The  $(c, \nu)$  parameter plane. The grey region corresponds to parameter values for which the condition (15) is fulfilled, i.e. where a peak in the SAD is present. The symbols correspond to parameters as in the simulations shown in (A) but for the neutral value  $c = 0$  here not represented.

from neutrality  $c$ , and constitutes our central result. In order to interpret  $p_k$  as the SAD we have to impose the normalization condition  $\sum_{k=1}^{\infty} kp_k = J$ . As shown in the Appendix, this normalization leads to the following exact expression for the biodiversity number

$$\theta = \frac{J\nu}{g(1-\nu)}. \quad (13)$$

In the neutral limit ( $c = 0$ ), we have  $g = 1$  so that  $\theta$  is equal to the neutral value  $J\nu/(1-\nu)$  and the SAD (12) reduces to the Fisher log-series (Hubbell, 2001; Volkov et al., 2003). Conversely, in the general case  $c \neq 0$ ,  $g > 1$  and the biodiversity number is enhanced by with respect to the neutral case due to competition. In the Appendix, we show that the unknown quantity  $g$  can be obtained as the solution of the transcendental equation

$$\frac{1-\nu}{\nu} = \operatorname{erfc}\left(\frac{3c - 2\ln(g(1-\nu))}{2\sqrt{2c}}\right) e^{\frac{[c-2\ln((1-\nu)g)]^2}{8c}}. \quad (14)$$

In Figure 1A we show SADs from the model at  $\nu = 10^{-3}$  and different values of  $c$  as indicated by symbols in the  $c, \nu$  plane shown in Fig. 1B, with the addition of the neutral value  $c = 0$  not represented therein. In all cases, numerical data (symbols) are in excellent agreement with the analytical prediction (12) represented in solid lines, validating the self-consistent approach.

For small values of  $c$ , the SAD is monotonically decreasing with  $n$ , similarly to the (neutral) Fisher log-series but for faster (Gaussian) fall-off for large populations. Interestingly, for larger values of  $c$ , SAD curves develop a maximum at a finite number of individuals, as emphasized in the inset of Fig. 1A. A study of the function (12) reveals that the condition for developing a maximum at  $n > 1$  is

$$\frac{c}{2} + \ln(g(1-\nu)) - 2\sqrt{c} > 0, \quad (15)$$

corresponding to the shaded area in Fig. 1B.

We now discuss how the average number of species  $\langle S \rangle = \sum_k p_k$  depends on the deviation from neutrality. As this

number is proportional to the number of individuals  $J$ , in Fig. 2A we plot the fraction  $\langle S \rangle/J$  as a function of the speciation rate  $\nu$  and the intensity of competition  $c$ . For any fixed value of the speciation rate  $\nu$ , the average number of species grows with  $c$ , meaning that the system is able to sustain a larger diversity with respect to the neutral case thanks to the stabilizing effect of niches. In Fig. 2B, we compare the prediction obtained by summing the terms of Eq. (12) with numerical simulation of the model, again showing an excellent agreement between theoretical prediction and simulation of the stochastic model.

### 3.2. Species extinction times distribution

We now focus on dynamical, rather than static, patterns which provide useful information on the differences between neutral and non-neutral theories (Pigolotti et al, 2005; Azaele et al, 2006; Allen and Savage, 2007; Bertuzzo et al., 2011). In particular, it is interesting to compare features of the dynamical balance between species introduction, and extinction as a function of the competition strength  $c$ . As in the model species originate from a single individual, we are interested in the statistics of the time it takes for a new species (introduced via a single individual) to become extinct. The results are presented in unit of generations, meaning that  $t = 1$  corresponds to  $J$  iteration steps of the model of Sec. 2.

In the neutral case  $c = 0$ , by applying ideas from the theory of branching processes (Harris , 1989), it is possible to derive an analytical expression for the probability of a species to survive a time  $t$  (from the time of its introduction in the system), which is given by (Pigolotti et al, 2005)

$$p_e(t) = \left(\frac{\nu}{e^{\nu t} - 1 + \nu}\right)^2 e^{\nu t}. \quad (16)$$

For  $\nu \ll 1$ , such distribution displays a power-law tail  $t^{-2}$ , followed by an exponential cutoff set by  $\nu$ . Notice

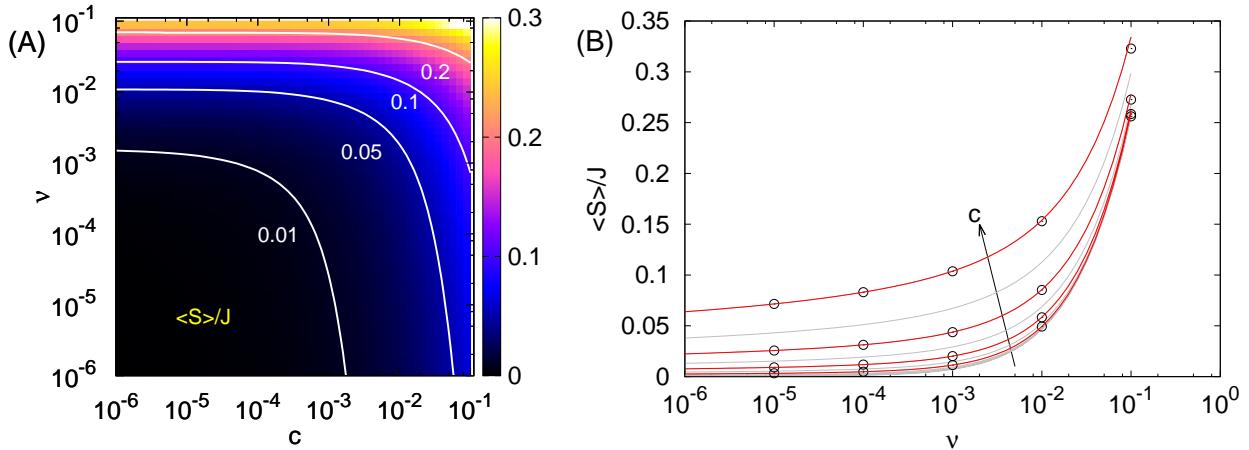


Fig. 2. (A) Average number of species normalized by the community size,  $\langle S \rangle / J$ , in the  $(c, \nu)$  parameter space, as predicted by summing the terms of Eq. (12). (B) Same quantity as a function of  $\nu$  for different values of  $c$ , increasing in the arrow direction. Symbols are results from simulations, in excellent agreement with the prediction in red lines. Grey lines correspond to values of  $c$  different from those of the simulations.

that the power-law  $t^{-2}$  can be modified by dispersal properties different from the global one here considered (Bertuzzo et al., 2011). For  $c > 0$ , no closed expression for the extinction-time distribution is available. Indeed, also a simple quadratic nonlinearity in the birth (or death) rates for a single species makes the problem analytically intractable, but for clever approximations as discussed in a series of works (see, e.g. Norden, 2001; Newman et al., 2004; Doering et al., 2008; Parsons et al., 2008). For this reason, we limit ourself to a numerical study. In Figure 3, we show the extinction-time distribution,  $p_e(t)$ , for different values of  $c$  fixing  $\nu$ . Increasing  $c$  has a non-trivial effect on the shape of the extinction-time distribution.

Qualitatively, one can identify three regimes. At short times, the distribution is only weakly dependent on  $c$ , i.e. by the presence of competition, and essentially reproduces the neutral result. At intermediate times, the extinction-time probability increases with  $c$ . Finally, at large extinction times it decreases with  $c$  by developing an exponential cutoff much steeper than predicted by formula (16). Fitting the exponential rate of decrease suggests a dependency of extinction probability of the form  $p_e(t) \sim c^{-\alpha t}$ , at least for small  $c$  (inset of Fig. 3).

As suggested by niche-stabilization arguments, the net effect of these different regimes on the average extinction time is always positive: the average lifetime of a species in our model is a growing function of  $c$  (see Fig. 4), which can exceed up to 2 or 3 order of magnitude (depending on  $\nu$ ) the neutral value

$$\langle t \rangle = \frac{\ln(1/\nu)}{1 - \nu}, \quad (17)$$

derived from Eq. (16). It is interesting to notice that, while enhancing the intensity competition (larger  $c$ ) increases the average extinction time, it decreases its relative fluctuations as confirmed by the behavior of the coefficient of variation,  $CV = \sqrt{\langle t^2 \rangle - \langle t \rangle^2} / \langle t \rangle$ , shown in the inset of Fig. 4. This means that, while in the neutral case when  $\nu \ll 1$  extinction times can vary greatly around the average value,

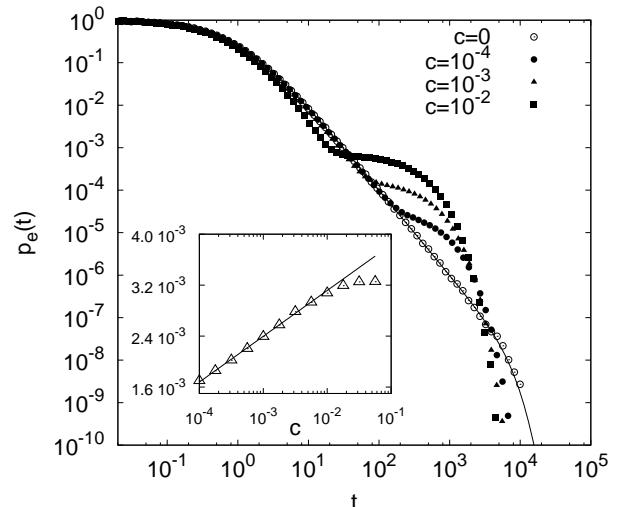


Fig. 3. Probability density function,  $p_e(t)$ , of the extinction times for  $J = 10^4$ ,  $\nu = 5 \cdot 10^{-4}$  and different values of the competition parameter  $c$ , as in the legend. For  $c = 0$  the prediction of (16) is perfectly verified. Inset: behavior of the exponent of the exponential tail of pdf as a function of  $c$ . The solid line displays the fit  $a \ln(c) + b$  with  $a \approx 0.000312$  and  $b = 0.000455$ .

niche stabilization has also the effect of making the average time a better prediction for the lifetime of a randomly chosen species.

#### 4. Discussions

We studied a community model incorporating neutral demographic stochasticity with niche stabilization. The model belongs to a general class of niche-neutral models discussed in the recent literature (Gravel et al., 2006; Adler et al., 2007) and, in particular, is built upon two specific models originally proposed by Haegeman and Loreau (2011); Noble et al. (2011b); Noble and Fagan (2011c). We assumed that violation of neutrality is controlled by

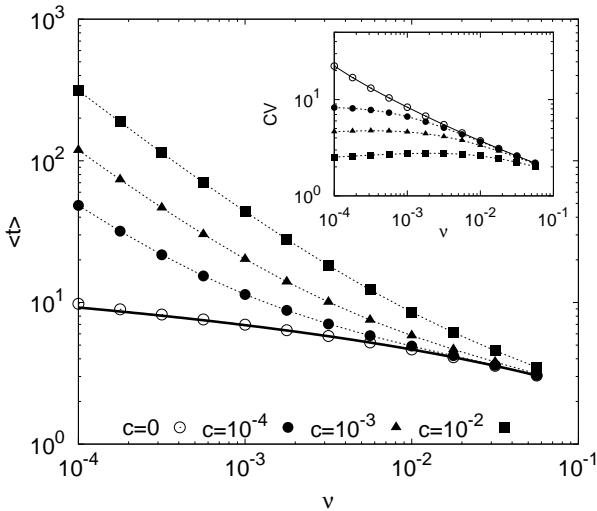


Fig. 4. Average extinction time as a function  $\nu$  for different values of  $c$ , as in the legend. For  $c = 0$ , the prediction of Eq. 17 perfectly agrees with the data. Inset: coefficient of variation of the extinction time, defined as  $CV = (\langle t^2 \rangle - \langle t \rangle^2)^{1/2} / \langle t \rangle$ , as a function of  $\nu$  for the same values of  $c$ .

a single parameter,  $c$ , weighting the relative intensity of intra- versus interspecific competition. We focused on the case in which effects of interspecific interactions are weak compared with intraspecific ones (i.e.  $c > 0$  in our model), a feature well supported by data (see, e.g., Condit et al., 1992; Harms et al., 2000; Volkov et al., 2009) and by mechanisms such as the well known Janzen-Connell effects (Janzen, 1970; Connell, 1971). For the sake of simplicity, as in (Haegeman and Loreau, 2011), we assumed that, even in non-neutral cases, species are symmetric and with no intrinsic fitness advantages. The model depends also on rate  $\nu$  of introduction of new species by speciation or immigration.

We proposed a self-consistent calculation which allowed us to straightforwardly derive an analytical expression for the species abundance distribution, Eq. (12). Self-consistency avoids some of the problems of other approaches like perturbative techniques, where one has to figure out the relative magnitude of the two small parameters  $\nu$  and  $c$ . While we focused here on one specific source of non-neutrality, one can expect that other non-neutral (symmetric) models can be solved using similar ideas. Indeed, species permutation symmetry is the crucial assumption to compute the SADs, rather than the specific way niches are introduced. However, we remark that even in the presence of species permutation symmetry, the self-consistent ansatz may not lead to the correct result when this symmetry is spontaneously broken (Borile et al., 2012).

Interestingly, in a large portion of the parameter space  $(c, \nu)$ , the relative abundance distribution curves show a maximum for intermediate abundance classes, similarly to many instances of SAD curves measured on the field (Hubbell, 2001). Specifically, such mode appears when intraspecific competition parameter  $c$  exceeds a critical value (predicted by Eq. (15)) depending on the rate  $\nu$  of intro-

duction of new species. We remind that spatially implicit implementations of the neutral model, which include some level of dispersal limitation, have been shown to provide very good fit of such field-measured SAD curves (Hubbell, 2001; Volkov et al., 2003). Without dispersal limitation, good fits have been obtained by combining neutral community models with specific forms of density-dependent reproduction rates (Volkov et al., 2005).

Within the model here investigated, the presence of a peak in SAD curves corresponds to the natural emergence of an effective carrying capacity for each niche, so that the population of each species fluctuates around a well defined average value. It should be remarked, however, that the tail of the SAD distribution, i.e. the probability of encountering a very abundant species, falls off in a much sharper way for large  $n$  than in Hubbell's spatially-implicit neutral model, due to the presence of a term proportional to  $\exp(-cn^2)$  in Eq. (12). Typical datasets well fitted by the neutral theory (Hubbell, 2001; Volkov et al., 2003) support the presence of a fatter log-normal-like tail. As a consequence, best fits of those datasets with formula (12) (not shown) are biased by such long tails and are thus realized close or at the neutral limit (i.e. for  $c \rightarrow 0$ ), where the peak disappears.

The emergence of this Gaussian cutoff, conflicting with classic datasets, is likely due to the fact that the niche-stabilization mechanisms incorporated in our model are particularly strong in the absence of dispersal limitation. It is indeed reasonable to expect that the sharp fall-off should be a quite general feature for global dispersal models in which an effective carrying capacity for any single species emerges and should not depend too much on model details. We conjecture that including some form of dispersal limitation with a competition acting on a finite range may lead to fatter tails. Similar features were observed in Chave et al. (2002) while comparing global and limited dispersal models with density dependence or other stabilizing mechanisms, such as tradeoffs. In this perspective, it would be interesting to extend the model to incorporate, even in a spatially implicit form, some degree of dispersal limitation. Unfortunately, this extension makes the analytical treatment much harder and it is left for future investigations. Another way fatter tails may arise would be to break the symmetric hypothesis and letting different species having different carrying capacity.

Studying dynamic patterns of species lifetimes (Sect. 3.2) revealed that the main effect of violating neutrality is to suppress the large fluctuations of lifetimes, typical of neutral dynamics (Pigolotti et al., 2005). On the one hand, enhanced self-competition prevents the possibility of a species to achieve a very large population size and thus lifetimes much longer than the average, which are exponentially suppressed. Similar exponential distributions of lifetimes have been observed in fossil data, a fact often explained in terms of the Red Queen effect in a changing environment (Van Valen, 1973). On the other hand, a species is favored when rare making it less prone to extinction by demographic stochasticity when its population is small. These effects are

weighted by the competition parameter, as a result the average species lifetime results increased with respect to the neutral expectation (17).

As observed by many authors (see, e.g. Lande et al, 2003; Ricklefs, 2003; Nee, 2005; Ricklefs, 2006; Allen and Savage, 2007), one of the problem with the neutral theory relies on the fact that average species lifetimes are typically too short, up to some order of magnitude, compared to those estimated from fossil records. The origin of such discrepancy is likely due to the point speciation mode, typically implemented in neutral models (Hubbell, 2003). As suggested by Allen and Savage (2007), a possible way-out for overcoming this problem is to allow for larger incipient-species abundances. Moreover, the same authors have also shown that allowing for some environmental stochasticity can decrease the lifetime of very abundant species, which is another issue with the neutral prediction for the species lifetimes distribution.

Furthermore, our model shows that niche-stabilization induced by intraspecific interactions larger than interspecific ones, for a given value of  $\nu$ , both increases the average lifetime (up to 2 or 3 order of magnitudes depending on  $\nu$  and  $c$ ) and suppresses large fluctuations. In particular, the smaller the value of  $\nu$ , the larger is the effect of competition. Thus, competition allows the system to sustain a larger diversity (Fig. 2) of longer-lived (Fig. 4) species with respect to a purely neutral community and, at the same time, suppressing the probability of species with exceedingly large lifespan with respect to the average.

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## Appendix A. Computing $g$ and $\theta$

Here, we derive the expression for the normalization  $\theta$  presented in Eq. (13), and discuss a semi-analytical method to estimate the parameter  $g$ , which is self-consistently defined as

$$g = g(c, \nu) = \frac{\tilde{p}'(0)}{\tilde{p}'(c)} = \frac{\sum_{k=1}^{\infty} (1-\nu)^k g^k e^{-\frac{c}{2}k(k-1)}}{\sum_{k=1}^{\infty} (1-\nu)^k g^k e^{-\frac{c}{2}k(k+1)}}. \quad (\text{A.1})$$

For the sake of notation simplicity we denote with  $\mathcal{N}$  and  $\mathcal{D}$ , respectively, the numerator and denominator in the right hand side of expression (A.1). By rearranging the indices in the summations, one can show that they satisfy

$$\mathcal{D} = \frac{\mathcal{N} - g(1-\nu)}{g(1-\nu)}. \quad (\text{A.2})$$

Substituting (A.2) into (A.1) yields an expression for  $\mathcal{D}$ :

$$\mathcal{D} = \sum_{k=1}^{\infty} (1-\nu)^k g^k e^{-ck(k+1)/2} = \frac{1-\nu}{\nu}. \quad (\text{A.3})$$

The normalization  $\theta$  can be then derived by imposing the condition  $\sum_k kp(k) = J$ . By direct substitution, one obtains  $\sum_k kp(k) = \theta \mathcal{N}$ . Then, using the fact that  $\mathcal{N} = g\mathcal{D} = g(1-\nu)/\nu$  yields the result (13).

Let us now discuss how estimating  $g$  in the relevant parameter range of  $c \ll 1$  and  $\nu \ll 1$ . In such limit, one can approximate very closely the series in (A.3) with an integral

$$\frac{1-\nu}{\nu} \approx \int_1^{\infty} dk (1-\nu)^k g^k e^{-\frac{c}{2}k(k+1)} = \sqrt{\frac{\pi}{2c}} \quad (\text{A.4})$$

$$\operatorname{erfc}\left(\frac{3c - 2\ln(g(1-\nu))}{2\sqrt{2c}}\right) \exp\left\{-\frac{[c - 2\ln((1-\nu)g)]^2}{8c}\right\}$$

Equating the first and the last term in the above expression leads to Eq. (14), that can be solved for  $g$  semi-analytically by standard methods. The dependence of  $g$  on  $\nu$  and  $c$  is shown in Fig. A.1.

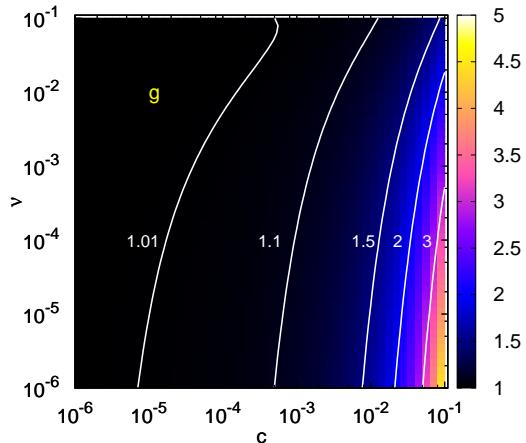


Fig. A.1. Contour plot of the quantity  $g$  in the  $(c, \nu)$ -plane, as computed by solving Eq. (14) semi-analytically.

We conclude by discussing possible analytical expressions for  $g$ . In the neutral limit of  $c = 0$ , one has  $g = 1$ , it is thus tempting to build up an expansion to obtain a closed expression for  $g$  at least in the limit  $c \ll 1$ . However, such expansion in Eq. (A.4) requires additional assumptions on the relative magnitude of the two small parameters  $c$  and  $\nu$ . For example, the argument of the error function is very small when  $\nu \ll c \ll 1$ , but very large when  $c \ll \nu \ll 1$ , so that in the first case a Taylor expansion is appropriate, while in the second one has to perform an asymptotic expansion. More formally, one can show that the function  $g(\nu, c)$  is not analytic at the point  $\nu = c = 0$ , so that one can not perform a Taylor expansion in the two small parameters. This also suggests that, more in general, other near-neutral models can be hard (or impossible) to treat with perturbative methods due to the interplay between the two small parameters.

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